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FEEDING PATTERN OF *HELICOVERPA ZEA* (BODDIE) CATERPILLARS ON FLOWERS OF *GNAPHALIUM ROBUSTUM* PHIL.[1]

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ABSTRACT

The feeding pattern of *Helicoverpa zea* caterpillars on flowers of *Gnaphalium robustum* was assessed by comparing the number of flowers eaten with the total number of flowers in a glomerule, and by observing several behavioral sequences. Caterpillars ate only a small number of flowers (2.7 ± 0.2) compared to the total number of flowers in a glomerule (15.2 ± 1.5), and they did not return to feed on the same glomerule. A "dispersed feeding" pattern was found and the use of chemical cues for the selection of glomerules was proposed. Two predictions were tested: i) *H. zea* caterpillars should reject eaten glomerules, either by the same caterpillar or by a conspecific, and ii) *H. zea* caterpillars should reject glomerules with frass, either of the same larvae or of a conspecific. Both predictions were confirmed.
Key words: *Helicoverpa zea*, *Gnaphalium robustum*, caterpillars, glomerules, feeding pattern, chemical cues, induced responses.

RESUMEN

Se evaluó el patrón de alimentación de orugas de *Helicoverpa zea* sobre flores de *Gnaphalium robustum*, comparando el número de flores comidas con el número total de flores por glomérulo y observando diferentes secuencias de comportamiento. El número de flores que comen las orugas fue pequeño (2.7 ± 0.2), en comparación con el número total de flores por glomérulo (15.2 ± 1.5), y nunca regresaron a comer en el mismo glomérulo. Se observó un patrón de "alimentación dispersa" y se propuso la utilización de señales químicas para la selección de los glomérulos. Se pusieron a prueba dos predicciones: i) las orugas de *H. zea* deberían rechazar los glomérulos comidos, ya sea por la misma oruga o por un conespecífico, y ii) las orugas de *H. zea* deberían rechazar los glomérulos con fecas, ya sean de la misma oruga o de un conespecífico. Ambas predicciones fueron confirmadas.
Palabras claves: *Helicoverpa zea*, *Gnaphalium robustum*, orugas, glomérulos, patrón de alimentación, señales químicas, respuestas inducidas.

INTRODUCTION

Caterpillars often show preference for feeding on plant parts that are easy to chew and digest, high in nutrients and water, and low in allelochemicals (Slansky & Scriber, 1985). Amongst other explanations, dispersed feeding in insects may be interpreted as a way to avoid induced responses of the plant which are deleterious to the insect. Preliminary observations in the Río Clarillo National Reserve suggest that inflorescences of *Gnaphalium robustum* Phil. (Asteraceae) suffer disperse feeding, i.e. often only a small proportion of the flowers contained in a glomerule appears with feeding damage. The damage is caused by the caterpillar of the moth *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae). The feeding pattern of *H. zea* on *G. robustum* was further studied to test the following hypotheses: 1) dispersed damage in

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glomerules of *G. robustum* is produced by caterpillars' behavior; and 2) caterpillars use the presence of frass as a cue for rejection of damaged glomerules.

METHODS

Helicoverpa zea (Lepidoptera : Noctuidae) is a moth which in its larval stages (caterpillars) is a major pest affecting many crop species worldwide because of its generalist habit. In Chile it is an introduced species which is found in wild plant species. In Río Clarillo National Reserve (33° 51´ S - 70° 29´W, 45 km southeast of Santiago, Chile) it was found feeding on *Gnaphalium robustum* (Asteraceae), an annual or biannual herb found in degraded lands and sunny slopes. Flowering occurs from october to march. Flowers are white, small, and are arranged in glomerules.

The feeding pattern of *H. zea* was determined by comparing the number of flowers eaten and the total number of flowers in each of 46 glomerules sampled. Each glomerule belonged to a different plant. The Spearman correlation test was applied.

Twenty-three observations were made on the feeding behavior of the caterpillars. The behavioral patterns were determined by counting the number of observations for each of the three behavioral sequences described in Table 1.

In order to test the rejection by caterpillars of partially eaten glomerules, actively eating caterpillars (1.5 to 2.0 cm long) were collected and subjected to fasting for two hours. Thereafter, they were allowed to feed on intact glomerules until they moved and fed in another glomerule, thus making sure caterpillars left the glomerule for reasons other than satiation. They were again collected and subjected to fasting for two additional hours. Finally, caterpillars were assigned to three different groups, which fed on: i) the same glomerules each caterpillar ate before, ii) glomerules that were eaten by a conspecific, and iii) not eaten glomerules (control group). Each of these groups were tested in a different day.

In order to test the rejection of glomerules with frass, actively eating caterpillars (1.5 to 2.0 cm long) were collected, subjected to fasting for two hours, and thereafter assigned to two different groups, which fed on: i) intact glomerules with frass of the same caterpillar, and ii) intact glomerules with frass of a conspecific. The control group of the previous experiment was used as control. Each of these groups were tested in a different day.

Comparisons between groups of the rejection experiments were made using the two tailed Fisher Exact Test. Due to multiple comparisons, the Bonferroni correction was applied. Differences were considered significant when the *P*-value was less or equal to 0.0125.

RESULTS

The number of flowers eaten by *Helicoverpa zea* caterpillars on glomerules of *Gnaphalium robustum* was 2.7 ± 0.2 with a range of 1 to 5 flowers, while the total number of flowers in a glomerule was 15.2 ± 1.5 with a range of 4 to 40 flowers ($r_{Spearman} = 0.081$, $P = 0.63$).

The number of observations for each of the three behavioral sequences of *H. zea* caterpillars feeding on glomerules of *G. robustum* showed that caterpillars did not return to eat in the same glomerule they were eating before (Table 1).

The experiments of food selection behavior by *H. zea* caterpillars showed that they rejected glomerules previously eaten both by the same caterpillar or a conspecific, and that they also rejected glomerules with frass of both of the same caterpillar or a conspecific (Table 2).

DISCUSSION

The feeding pattern of *Helicoverpa zea* caterpillars on glomerules of *Gnaphalium robustum* and their behavioral sequence clearly suggest a food selection behavior, i.e. caterpillars eat a small number of flowers within a glomerule and then move away to feed in another glomerule (Table 1). They also reject damaged glomerules, regardless if it is a glomerule previously eaten by the same caterpillar or a conspecific (Table 2).

The latter results also suggest the release of chemicals from the damaged glomerules which may be acting as a cue for the caterpillars to reject those previously eaten. Alternatively, rejection of glomerules with frass, either their own or that of a conspecific, also suggests the presence of some chemical in the frass which may be used by the caterpillars as an indirect cue to reject previously eaten glomerules.

TABLE 1
BEHAVIORAL SEQUENCE OF *HELICOVERPA ZEA* CATERPILLARS FEEDING ON GLOMERULES OF *GNAPHALIUM ROBUSTUM*

Question	Behavioral sequence	Observations	Answer
Do caterpillars move to feed in another glomerule after have been feeding?	F → F*	12	Yes
Do caterpillars move to feed in another glomerule after have been resting?	F → R → F*	11	Yes
Do caterpillars continues feeding in the same glomerule after have been resting?	F → R → F+	0	No

F : feeding in a glomerule, F* : feeding in another glomerule, R : rest, F+ : feeding in the same glomerule.

TABLE 2
REJECTION OF GLOMERULES OF *GNAPHALIUM ROBUSTUM* BY *HELICOVERPA ZEA* CATERPILLARS

Question	Contrast	*P*-value*	Answer
Do caterpillars reject glomerules previously eaten by themselves?	EATo vs CON	0.0013	Yes
Do caterpillars reject glomerules previously eaten by a conspecific?	EATc vs CON	0.0001	Yes
Do caterpillars reject glomerules with presence of their own frass?	FRAo vs CON	0.0038	Yes
Do caterpillars reject glomerules with presence of a conspecific frass?	FRAc vs CON	0.0060	Yes

CON : feeding on not eaten glomerules, EATo : feeding on glomerules eaten by the same caterpillar, EATc : feeding on glomerules eaten by another caterpillar, FRAo : feeding on glomerules with frass of the same caterpillar, FRAc : feeding on glomerules with frass of another caterpillar.
*Fisher Exact Test. Differences between groups are considered significant when the *P*-value is less or equal to 0.0125, according to the Bonferroni correction for multiple comparisons.

At least four possible explanations can account for this food selection behavior of *H. zea* caterpillars: i) they look for more palatable flowers (i.e. more easy to chew and digest, high in nutrients or water, or showing a different allelochemical profile), ii) they avoid induced responses which may decrease the palatability of flowers, iii) they avoid intraspecific competition, and iv) they avoid natural enemies that could be attracted by plant volatiles released upon damage.

Concerning the first hypothesis, it was observed that damaged flowers within a glomerule very often occur one next to the other. Hence, there appears to be no selection process in the movement between flowers.

The second hypothesis may explain the rejection of previously eaten glomerules by *H. zea* caterpillars, given that results refute satiation as the cause of caterpillar's rejection of attacked flowers; instead, observations indicate that a change in the quality of the food occurs after *H. zea* feeding (i.e. an induced response: Karban & Baldwin, 1997).

The hypothesis of avoidance of intraspecific competition is sustained by the observation of agressiveness among *H. zea* caterpillars when two of them meet and at least one of them is feeding. This behavior has been well described for caterpillars of *H. zea* (Artigas, 1994). From this point of view, rejection of both previously eaten glomerules and glomerules with frass, would be a caterpillar's response to cues indicating possible proximity of a conspecific.

In support of the last hypothesis, there is evidence on natural enemies of caterpillars (i.e. predators and parasitoids) being attracted by damaged plants (Dicke & Sabelis, 1988, Dicke *et al.*, 1990, Steinberg *et al.*, 1993, Turlings *et al.*, 1995), and also on defensive behaviors of caterpillars, such as moving away from the feeding site (Slansky, 1993). In the present case, this hypothesis is weakened by the fact that *H. zea* caterpillars are observed resting in the vicinity of attacked glomerules.

Even if some of the hypotheses presented appear more likely than others, it should be pointed out that the observed food selection behavior of *H. zea* caterpillars might well be the result of the interaction between these phenomena.

Further studies are needed to clarify the reasons underlying food selection behavior of *H. zea* caterpillars feeding on flowers of *G. robustum*. It would be specially rewarding to study the chemical variation of flowers within a glomerule, as well as the chemical variation of glomerules within and among plants after feeding damage. It is also necessary to address dietary changes upon aging of caterpillars, as well as the costs and benefits of moving to other glomerules instead of remaining feeding on the same glomerule until all its flowers are consumed.

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